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Diffusive gas transport through flooded rice systems

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Abstract. A fully mechanistic model based on diffusion equations for gas transport in a flooded rice system is presented. The model has transport descriptions for various compartments in the water-saturated soil and within the plant. Plant parameters were estimated from published data and experiments independent of the validation experiment. An independent experiment is described in which the diffusion coefficient of sulfurhexafluoride (SF_6) in water-saturated soil was determined. The model was validated by experiments in which transport of SF_6 through soil and plant was monitored continuously by photoacoustics. The independent default settings could reasonably predict gas release dynamics in the soil-plant system. Calculated transmissivities and concentration gradients at the default settings show that transport within the soil was the most limiting step in this system, which explains why most gases are released via plant-mediated transport. The root-shoot interface represents the major resistance for gas transport within the plant. A sensitivity analysis of the model showed that gas transport in such a system is highly sensitive to the estimation of the diffusion coefficient of SF_6, which helps to understand diel patterns found for greenhouse gas emissions, and to the root distribution with depth. This can be understood from the calculated transmissivities. The model is less sensitive to changes in the resistance at the root-shoot interface and in the root fraction active in gas exchange. The model thus provides an understanding of limiting steps in gas transport, but quantitative predictions of in situ gas transport rates will be difficult given the plasticity of root distribution.

1. Introduction

Rice is one of the most important crops in the world. By far most of the rice production, 86% [*Neue and Roger*, 1994], takes place under temporary or continuous flooding. Under these flooded conditions, gas transport is hampered and oxygen depletion develops quickly. Maintenance of oxygen transport through the rice plant is crucial for survival and rice plants adapt to this situation by the development of aerenchyma, both in roots and in shoots.

Gas transport through rice plants occurs, contrary to many other wetland plants [*Allen*, 1997], predominantly by diffusion and not by convection (T.T. Groot et al., Gas transport through rice tillers, submitted to *Plant, Cell and Environment*, 2001) (hereinafter Groot et al., 2001). Gases exchange via diffusion between the water-saturated soil and the root. This exchange mainly occurs at the root tip and through openings around lateral roots [*van Noordwijk and Brouwer*, 1993; *Flessa and Fischer*, 1992]. Both in roots and shoots, gases diffuse via the gas phase through aerenchyma [*Ando et al.*, 1983]. At the root-shoot interface, both aerenchyma systems are separated by a region of porous plant material (Groot et al., 2001), that reduces gas diffusion between root and shoot [*Butterbach-Bahl et al.*, 1997]. The gases exchange with the atmosphere either at the stomata or at special micropores [*Nouchi and Mariko*, 1993].

The transport system of rice serves as a main conduit for the diffusion of various gases between the flooded soil and the atmosphere, e.g., of plant-produced ethylene [*Lee et al.*, 1981] and oxygen [*Jackson and Armstrong*, 1999]. Plant transport of oxygen to the roots and into the soil is very important for plant survival in order to create microaerophilic conditions in the rhizosphere for the detoxification of anaerobically produced compounds [*Kumazawa*, 1984] and for proper root respiration. Gases produced in the anaerobic soil, like N_2, CO_2, N_2O, and CH_4, flow to the atmosphere via this plant-mediated transport. Except for N_2, these gases are important greenhouse gases. Up to 90% of the methane emitted from rice paddies is exchanged through plant-mediated transport [*Nouchi et al.*, 1994; *Schütz et al.*, 1989].

It is thus important to quantify the mechanisms of gas transport in the plant-rhizosphere-anaerobic soil system. Various models have been published on oxygen transport within one root [*Armstrong and Beckett*, 1987; *Luxmoore et*

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al., 1970]. Plant-mediated transport of methane from rice paddies has been described by one fitted overall conductance value [*Hosono and Nouchi*, 1997]. The diffusion of gaseous compounds into the rhizosphere starting at the root surface was modeled by *Newman and Watson* [1977] and *Darrah* [1991a, 1991b]. A combination of all these concepts into one mechanistic model for gas transport through the various compartments in a water-saturated soil-plant system does not seem to exist, however.

Therefore this paper describes a mechanistic model of gas transport through a water-saturated soil-plant system. In the model, various plant compartments and soil layers are distinguished to compare the transmissivities of each compartment. The analysis of model behavior enables us to better understand and quantify the rate-limiting steps in gas transport. The model was validated by experiments in which the transport of a trace gas, sulfurhexafluoride (SF_6), was monitored and quantified. In this study, SF_6 was measured by photoacoustic which is a sensitive technique with a high time resolution. SF_6 is an inert gas and the signal is thus not influenced by interfering production or consumption processes within the soil-plant column. Our detailed mechanistic transport model can improve greenhouse gas emission models and plant physiological transport models by linking the transport model to (spatial explicit) treatment of production and consumption processes of specific trace gases.

2. Materials and Methods

2.1. Determination of the SF_6 Diffusion Coefficient in Soil

We determined the diffusion coefficient of SF_6 in water and soils with the setup depicted in Figure 1, as the diffusion coefficient of SF_6 in water and soils was unknown [*Langø et al.*, 1996]. Two milliliters of pure SF_6 was injected into a stirred bottom compartment containing water, where it diffused into the soil-water compartment through a 8-mm-thick filter with a porosity of 28% and pores of 100-160 μm, permeable to water and dissolved products but not to gas bubbles. The soil-water compartment contained a few centimeters of water-saturated soil topped with a water layer. The thickness of each layer was measured by a micrometer. Evaporated water replenished by gravity forces through a syphon connected to a supply vessel, providing a constant water level. Water-saturated N_2 gas flowing through the headspace with a rate of 1 L h^{-1} carried SF_6 to the detector. A Nafion® membrane tube to dry the gas flow and a 10-ml KOH column to trap CO_2 were installed in front of the detector.

The experiment was carried out with two different soil layer thicknesses, without replication. In the first experiment, the water-saturated soil was 2.55 cm thick and had 1.10 cm of water on top. In the second experiment a column with 1.09-cm water-saturated soil and 0.33 cm of water on top was used. The diffusion coefficient for SF_6 could be calculated from these two experiments (see section 3.2).

2.2. Model Validation

For model validation, a similar setup was used as described above for the determination of the diffusion coefficient of SF_6 in water and soil, but this time the column contained a soil-rice plant system (Figure 2). Rice (*Oryza sativa L.*) cultivar IR 72, a short-duration, photoperiod-insensitive high-yielding modern cultivar developed by IRRI, was used. Rice seeds germinated on petri dishes were double planted into large containers with a 17-cm-deep mixture of rice paddy soil collected in the Philippines supplemented with Dutch river clay containing a low amount of organic matter. Plant spacing was 20 cm, and the minimal distance between plants and the walls of the container was 12.5 cm. The plants were grown in a greenhouse in The Netherlands with a constant temperature of 26°C and a 12-hour dark/12-hour light regime. After 2 weeks, the seedlings were thinned to one plant per location in order to obtain uniform plant density.

At the start of a validation experiment, an undisturbed plant-soil core was taken from the container in the greenhouse (to avoid root growth along the walls of the core). The core, with a soil moisture content of 0.57 m^3 water m^{-3} soil, was installed into the setup (Figure 2). During the experiment, the plant was kept in 12-hour dark/12-hour light regime and a constant temperature of 22°C. Aluminium foil was attached around the core to obtain good light exposure to all sides of the plant. Two validation experiments were carried out, the first with a plant taken from the greenhouse 90 days after germination and the second with a plant of 103 days old.

Two milliliters of pure SF_6 was injected into the stirred

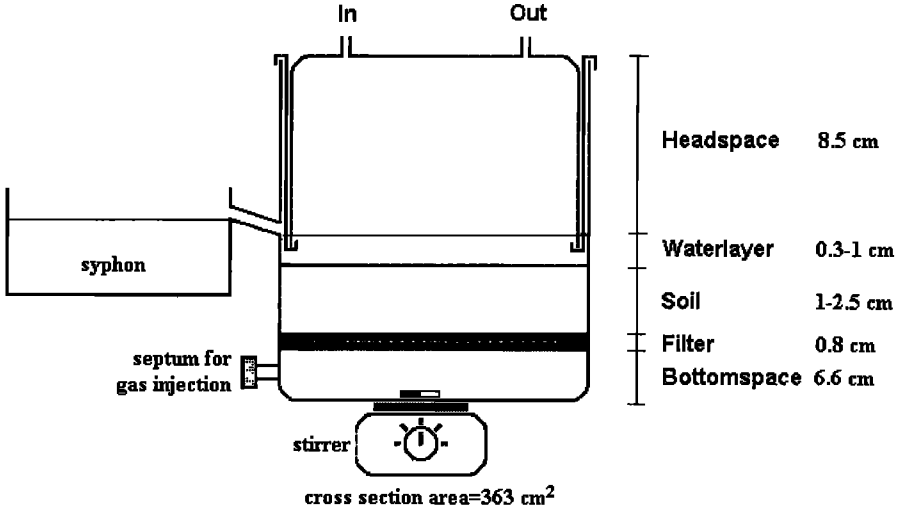

Figure 1. Setup for the determination of the diffusion coefficient of SF_6 in water. See text for full description.

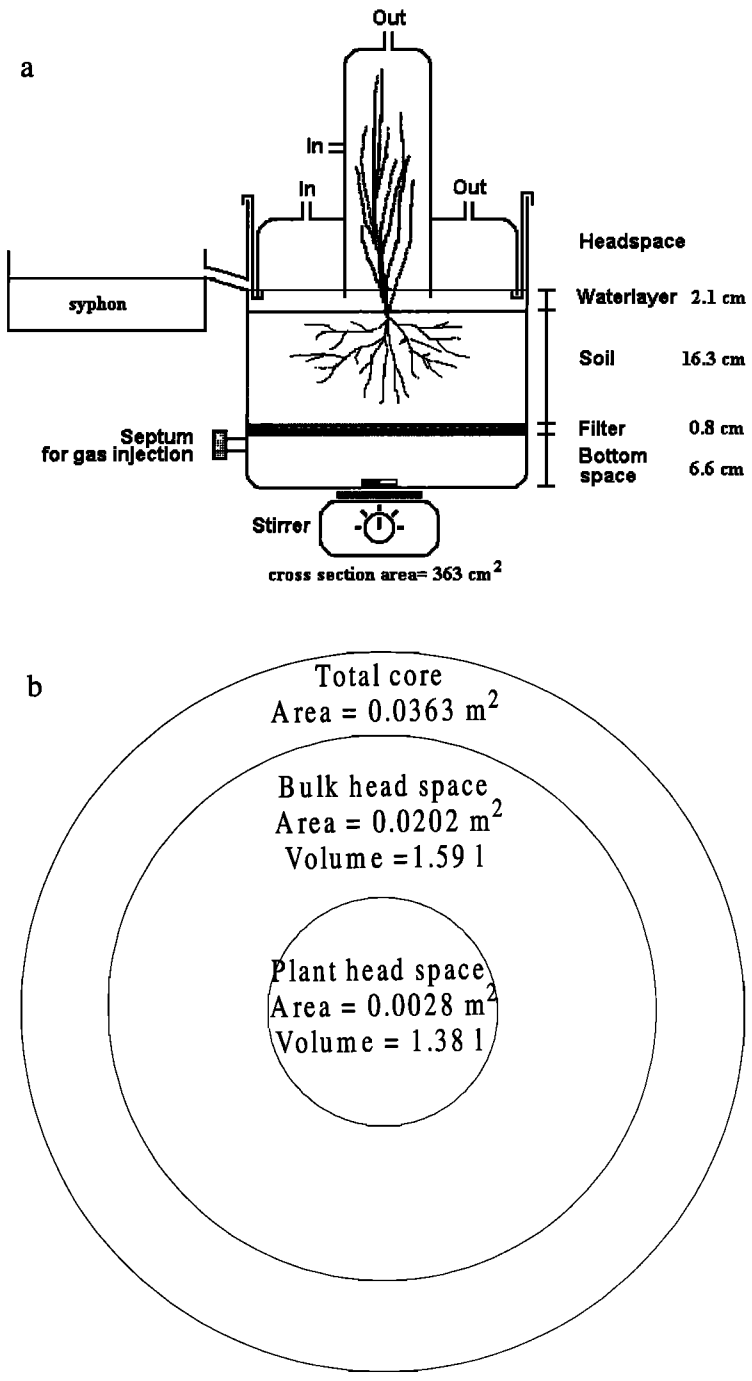

Figure 2. Setup for the model validation experiment: (a) side view and (b) top view.

bottom compartment which was full of water. From there it diffused through the same filter described above, the soil and via the plant into the headspace. Evaporated water was replenished by a syphon. Water-saturated air with a flow rate of 1 L h^{-1} was used as a carrier gas. CO_2 and H_2O traps were installed in front of the detector. SF_6 emission was monitored for 23 days and 16 days, respectively. Given the constant setup in the validation experiments, these experiments can be considered replicates. In this paper we present data from the central core depicted in Figure 2, which measures the fluxes from the rice plant and a small part of the diffusion from the soil. Given the small soil surface within the central core and given the slow diffusion through soil and water, the data are considered to be plant-mediated transport.

2.3. CO_2 Laser-based Trace Gas Detection

SF_6 concentrations were quantified by on-line CO_2laser-based trace gas detection. A CO_2laser has typically 90 laser lines in the infrared (wavelength 9-11 μm) region of the electromagnetic spectrum. All gases possessing high absorption strength combined with a characteristic absorption profile in the CO_2laser region can easily be detected by photoacoustics. The gas flow to be analyzed is guided through a detection cell through which a laser beam is

directed. By comparing the signals at different laser lines, the gas response can be separated from other interfering signals. When the laser irradiates the gas, the molecules may absorb photons and get excited into a higher rotational-vibrational state. This excitation energy is converted into kinetic energy of the molecules, i.e., heat. In our case the molecules are periodically excited with a CO_2laser in the infrared wavelength region by modulating the laser beam with a mechanical chopper at about 1 kHz. In the confined volume of the cell this causes a sound wave easily detectable by a microphone. The CO_2laser has a 40-cm-long gas discharge. The generated photoacoustic wave increases linearly with the incoming laser power. For this reason the low-noise photoacoustic cell is placed inside the laser cavity. To enhance the photoacoustic signal further, the detection cell is designed as an acoustic resonator, matching the chopper frequency. The electric signal coming from the microphone is fed into a lock-in amplifier to improve the signal-to-noise ratio and to filter out acoustical noise picked up by the microphone.

SF_6 gas has a strong rotational-vibrational *Q*band of the ν_3 vibration at 947.9 cm^{-1}. At atmospheric pressure, a large number of rotational lines of this band overlap with the CO_2laser line at 947.74 cm^{-1} resulting in an absorption strength of 0.85 $torr^{-1}$ cm^{-1} [*Cox and Gnauck*, 1980]. Our CO_2laser photoacoustic cell is able to detect SF_6 concentrations down to $5x10^{-3}$ ppbv.

2.4. Determination of Plant Characteristics

During the growth of the rice plants in the greenhouse, the dates at which a tiller formed was recorded and the tiller itself was labeled with small tags. Root length density was measured in rice plants grown in the same batch as the plants used in the model validation experiment. An undisturbed soil-plant core of 16 cm thick was harvested in the same week the validation experiment started. The whole core was frozen for a week at –20°C. The frozen soil core was sawn into four equally thick horizontal layers. Roots were washed and stored at 4°C in 17% acetic acid solution. Root length per soil layer was determined in duplicate by a Comair root length scanner, type HDH.

3. Model

3.1. Model Description

3.1.1. Transport. The basis of the model is the diffusion of gas (either in the gas phase or dissolved in water) through different compartments present in a soil-plant system. These compartments are the bottom space and filter (only incorporated in the model to allow comparison with our experimental setup), the soil, the stagnant water layer on top of the soil, the headspace, plant roots, and plant shoots. In the model, the soil and plant roots are divided into N vertical layers of equal thickness (N = 15 in the default model). The distribution of root length density with depth, which can have a profound influence on the changes in transport rates with depth and thus on the gas release rates, can be described by this vertical division. Transport through convective flows is neglected, as convective flows contribute little to the total water and solute transport in rice systems [*Denier van der Gon and van Breemen*, 1993; *de Willigen and van Noordwijk*, 1994]. The diffusive gas flows ($Flow_{i,j}$) across an interface (in mol/s) can be described with

$$Flow_{i,j} = \kappa_{i,j} \cdot ([C_j] - [C_i]). \quad (1)$$

Table 1. List of Symbols

Symbol	Description
A	cross-section area, m^2
$avg(RLD)$	total average root length density over the soil profile at time t, m m^{-3} soil
$[C]$	concentration in a compartment, mol m^{-3}
$D_{i,j}$	diffusion coefficient of SF_6, m^2 s^{-1}
DAT	time after transplanting the rice crop, s
F_{exch}	fraction of the root surface active in gas exchange, dimensionless
$Flow_{i,j}$	diffusive gas flow across interface i to j, mol s^{-1}
K_{til_no}	maximum tiller number-number of $tillers_{t=0}$/ number of $tillers_{t=0}$, dimensionless
K_{til_length}	maximum length-tiller bud $length_{t=0}$/tiller bud $length_{t=0}$, dimensionless
LAI	leaf area index, m^2 plant m^{-2} soil
m	empirical parameter for tortuosity, dimensionless
n	empirical parameter for tortuosity, dimensionless
N	total number of soil layers, dimensionless
R_l	radius of a plant compartment, m
$rel(RLD_x)$	relative root length density in soil layer x compared with $avg(RLD)$, dimensionless
$rgr_{til(length)}$	relative growth rate of tiller length, s^{-1}
$rgr_{til(no)}$	relative growth rate of number of tillers, s^{-1}
RLD_x	root length density in layer x, m m^{-3} soil
$z_{i,j}$	diffusion distance, m
α	Ostwald coefficient of SF_6, m^3 gas m^{-3} water
ε	gas-filled porosity of the medium, m^3 gas m^{-3} medium
$\kappa_{i,j}$	transmissivity of interface i to j, m^3 s^{-1}
θ	water-filled porosity, m^3 water m^{-3} soil
τ	tortuosity of the soil pores or roots, m m^{-1} medium
$\omega_{i,h}$	micropore conductance, m gas s^{-1}
$\omega_{r,t}$	conductance root-shoot interface,m^3 gas m^{-2} tiller s^{-1}
Subscripts	
a	air
b	bottom space
f	filter
h	headspace
r	root
s	soil
t	shoot
w	water
x	layer number

Table 1 lists the symbols: $\kappa_{i,j}$ is a transport parameter through a porous medium that combines diffusion coefficients and medium properties (explained below) and is expressed per volume water or per volume gas, depending on the medium; $[C]$ is expressed in the same volumetric medium units as the transmissivity and corrected for porosity, if necessary. The concentrations in the headspace, roots, and shoots are expressed in the gas phase, as this is the dominant transporting medium for these compartments. The concentrations are corrected by root porosity and shoot

porosity, respectively. Root porosity depends on rice variety [*Colmer et al.*, 1998], stage in the growing season [*van Noordwijk and Brouwer*, 1993], and the environment. In a more reduced environment, more aerenchyma is formed [Ota, 1970]. In the model, an average value for root porosity, ε_r, of 0.295 ± 0.02 m^3 air m^{-3} root is used, based on data presented by *Armstrong et al.* [1991], *Barber et al.* [1962], *Butterbach-Bahl et al.* [1997], *Colmer et al.* [1998], *Jensen et al.* [1969], *Kludze and Delaune* [1995a, 1995b], *Kludze et al.* [1993] and *Luxmoore et al.* [1970]. Shoot porosity, ε_t, is estimated at 0.39 m^3 air m^{-3} shoot [*Jensen et al.*, 1969; *Butterbach-Bahl et al.*, 1997]. In the soil, the dominant transport is via the water phase and is corrected via θ_s.

If compartments i and j have different media, then $\kappa_{i,j}$ is expressed in m^3 water s^{-1} and the concentration in the medium with the gas phase is corrected for the gas solubility by the Ostwald coefficient (α), which is calculated at the reference temperature from *Langø et al.* [1996]. Temperature dependence is calculated from the empirical equation and its parameterization given by *Wilhelm et al.* [1977].

Because $Flow_{i,j}$ (equation (1)) in rice paddies is determined by diffusion, $\kappa_{i,j}$ can be calculated in analogy to Fick's law:

$$\kappa_{i,j}=\frac{A_{i,j}\cdot D_{i,j}}{z_{i,j}} \tag{2a}$$

The exact formulation and dimensions for the diffusion coefficient, $D_{i,j}$, are described by equation (3). Equation (2a) applies to the transmissivity of the bottom space-filter interface ($\kappa_{b,f}$) with $z_{b,f}$ equal to half the filter thickness and $D_{b,f}$ equal to the effective diffusion coefficient in the filter (D_f) treated in equation (3'). This formulation is allowed, because the bottom space is continuously stirred and does not limit transport (diffusion distance zero). The filter, and all other compartments, has uniform properties and the diffusion distance is thus the distance up to the center of the filter, and the diffusion distance of all other compartments can be derived similarly. The interface between soil layers ($\kappa_{s,s}$) can be treated similarly, with $z_{s,s}$ as the soil layer thickness (from the center of one soil layer to the center of the next soil layer) and $D_{s,s}$ equal to the diffusion coefficient in soil (D_s), treated in equation (3). The transmissivity of the water-headspace interface ($\kappa_{w,h}$) has $z_{w,h}$ of half the water layer thickness (as diffusion resistance in the headspace can be neglected) and $D_{w,h}$ equal to the diffusion coefficient of SF_6 in water (D_w in m^2 water s^{-1}). Finally, the transmissivity between soil and roots ($\kappa_{s,r(x)}$) can also be treated this way with $z_{s,r(x)}$ half the distance between roots and $D_{s,r}$ the soil diffusion coefficient (D_s). Subscript x indicates the layer number. The formulation of $A_{s,r(x)}$ is treated below (equation (8)).

If the interface extends over two different media, then a weighted average of characteristics of both media is accounted for in $\kappa_{i,j}$:

$$\kappa_{i,j}=\frac{A_{i,j}}{z_i/D_i+z_j/D_j}. \tag{2b}$$

Such a formulation applies to the transmissivity between filter and soil ($\kappa_{f,s}$) (where z_f is half the filter thickness and z_s is half the soil layer thickness) and to the transmissivity between soil and water layer ($\kappa_{s,w}$) (where z_w is half the water layer height).

The transmissivity between roots in different soil layers ($\kappa_{r,r}$) accounts for different root cross-section areas ($A_{r(i)}$) in different layers, explained further in equation (11) (layer numbers are indicated with subscripts x and $x+1$, respectively):

$$\kappa_{r,r}=\frac{D_a}{z_r\cdot\left(\frac{1}{A_{r(x)}}+\frac{1}{A_{r(x+1)}}\right)}. \tag{2c}$$

The total root length of an individual root in a layer equals the soil layer thickness divided by root tortuosity (described by equation (9)) and z_r is half this root length (equation (10)).

While gases can diffuse normally through the plant via root aerenchyma and shoot aerenchyma, gas transport is retarded at two interfaces: the interfaces root-shoot and shoot-headspace. Tissue porosity is severely reduced at the root-shoot interface, imposing an additional resistance, and at the shoot-headspace the stomata or micropores introduce an additional resistance to diffusion.

The transmissivity of the root-shoot interface ($\kappa_{r,t}$) is described analogous to serially connected resistances:

$$\kappa_{r,t}=\frac{1}{\frac{1}{\omega_{r,t}\cdot A_t}+\frac{z_r}{D_a\cdot A_{r(1)}\cdot\varepsilon_{r(1)}}+\frac{z_t}{D_a\cdot A_t\cdot\varepsilon_t}}. \tag{2d}$$

The diffusion distance in a tiller, z_t, and the tiller cross-section area, A_t, are quantified below. The conductance at the root-shoot interface, $\omega_{r,t}$, seems an important limitation for gas transport through rice plants [*Butterbach-Bahl et al.*, 1997]. Various experiments were designed to estimate this conductance. The conductance was highly variable and was significantly affected by methodology, tiller position, and tiller age (Groot et al., 2001). The model uses an average value of $2.04.10^{-6}$ m^3 gas m^{-2} tiller s^{-1} (Groot et al., 2001) as a default value for the root-shoot conductance.

The transmissivity for the shoot-headspace interface ($\kappa_{t,h}$) is described with

$$\kappa_{t,h}=\frac{1}{\frac{1}{\omega_{t,h}\cdot A_s\cdot LAI\cdot\varepsilon_t}+\frac{z_t}{D_a\cdot A_t\cdot\varepsilon_t}}. \tag{2e}$$

Methane is known to be released from a rice plant via the micropores [*Nouchi and Mariko*, 1993], while CO_2 and O_2 are exchanged via the stomata. For simplicity, $\omega_{t,h}$ is given the value of the stomata conductance, which varies between 0.003 and 0.02 m gas s^{-1} [*Penning de Vries et al.*, 1989]. In the model a value of 0.007 is used. The Leaf Area Index (LAI) equals 4 for a well-developed rice plant canopy [*Penning de Vries et al.*, 1989].

3.1.2. Diffusion coefficients. All transport characteristics have now been described except for D_f and D_s. Both are complicated by the influence of tortuosities (the increase in pathway due to soil structure) and water and gas porosities. D_s (in m^3 water m^{-1} soil s^{-1}) is described by

$$D_S=\frac{\varepsilon_S\cdot D_a\cdot\tau_a}{\alpha}+\theta_S\cdot D_w\cdot\tau_w. \tag{3}$$

Tortuosities, τ, are described according to *Campbell* [1985], which gives the most suitable and most easily parameterized tortuosity model at anaerobic conditions:

$$\tau_a=m\cdot\varepsilon_S^{(n-1)} \tag{4a}$$

$$\tau_w=m\cdot\theta_S^{(n-1)}. \tag{4b}$$

The dimensionless empirical parameters m and n equal 0.9 and 2.3, respectively, for clayey soils [*Campbell*, 1985].

The filter is water-saturated and has a water content (θ_f) of 0.28 m^3 water m^{-3} filter. The tortuosity, τ_f, is however unknown and was determined according to a method

described below. This leads for the diffusion coefficient in the filter, D_f, to

$$D_f = \tau_f \cdot \theta_f \cdot D_w . \quad (3')$$

If a bulk concentration instead of a concentration in one of the phases is used in combination with an effective diffusion coefficient, as is done by *Stephen et al.* [1998], then a change in transport rates is predicted upon a change in total porosity or upon other discontinuities, whereas real concentrations and thus real transport do not change.

3.1.3. Plant characteristics. The plant influences several transport parameters: $z_{s,r(x)}$, the diffusion distance between roots, $\kappa_{r,r}$, the transmissivity between roots in different soil layers, $\kappa_{r,t}$, the transmissivity of the root-shoot interface, and $\kappa_{t,h}$, the transmissivity at the shoot-headspace interface. All these parameters are dynamic parameters and depend on root biomass: $z_{s,r(x)}$ is influenced directly by the number of roots, $\kappa_{r,r}$ via $A_{r(i)}$ and z_r; $\kappa_{r,t}$ and $\kappa_{t,h}$ are influenced via the dynamic parameters A_t and z_t.

3.1.3.1. Diffusion distance between soil and roots ($z_{s,r(x)}$). The diffusion distance between soil and roots is equal to half the distance between two roots. This distance depends on the root length density in a specific layer. Assuming that roots in a layer can be approached by randomly distributed infinite lines (assuming an infinitely small root radius), the average $z_{s,r}$ in soil layer x is (derived from *Ogston* [1958])

$$z_{s,r(x)} = \sqrt{\frac{-ln(0.5)}{\pi \cdot RLD_x}} . \quad (5)$$

Root length density (RLD_x) is calculated from

$$RLD_x = avg(RLD) \cdot rel(RLD_x) ; \quad (6)$$

avg(RLD) is calculated from equation (1) given by *van Bodegom et al.* [2000]. To estimate *rel(RLD$_x$)*, it is assumed that root lengths decrease exponentially with depth. The slope and intercept of the depth profile change during the growing season owing to root growth into deeper layers; *rel(RLD$_x$)* is given by

$$rel(RLD_x) = (a_1 + b_1 \cdot DAT) \cdot exp[-(a_2 + b_2 \cdot DAT) \cdot \frac{x}{N}] , \quad (7)$$

where DAT is days after transplanting the rice crop. The empirical parameters a_1, a_2, b_1 and b_2 describe the exponential function and are estimated from root length density data by *Beyrouty et al.* [1988], *Kang et al.* [1994], *Slaton et al.* [1990], and *Teo et al.* [1995], shown in Figure 3a; a_1, a_2, b_1 and b_2 equal 4.63 (-), 5.09 (-), -4.16 10^{-7} (s^{-1}), and -5.87 10^{-7} (s^{-1}), respectively, according to a minimum mean square error with observed data. The fit with r^2 = 0.62 was not significantly different from observed data, according to Student's t test ($P < 0.05$).

Estimates for *rel(RLD$_x$)* were compared with the measured root length density of the plant used in the first validation experiment (harvested 102 days after transplanting). The results (Table 2) are similar, and only estimated values for *rel(RLD$_x$)* are used in the remaining part of the paper.

3.1.3.2. Root characteristics, $A_{s,r(x)}$, $A_{r(x)}$, and z_r. The soil-root cross-section area over which diffusion takes place, $A_{s,r(x)}$, is given by

$$A_{s,r(x)} = F_{exch} \cdot number\,of\,roots_x \cdot 2 \cdot \pi \cdot R_r \cdot root\,length . \quad (8)$$

Gas exchange mainly occurs around the root tip of primary roots and along lateral roots [*Flessa and Fischer*, 1992].

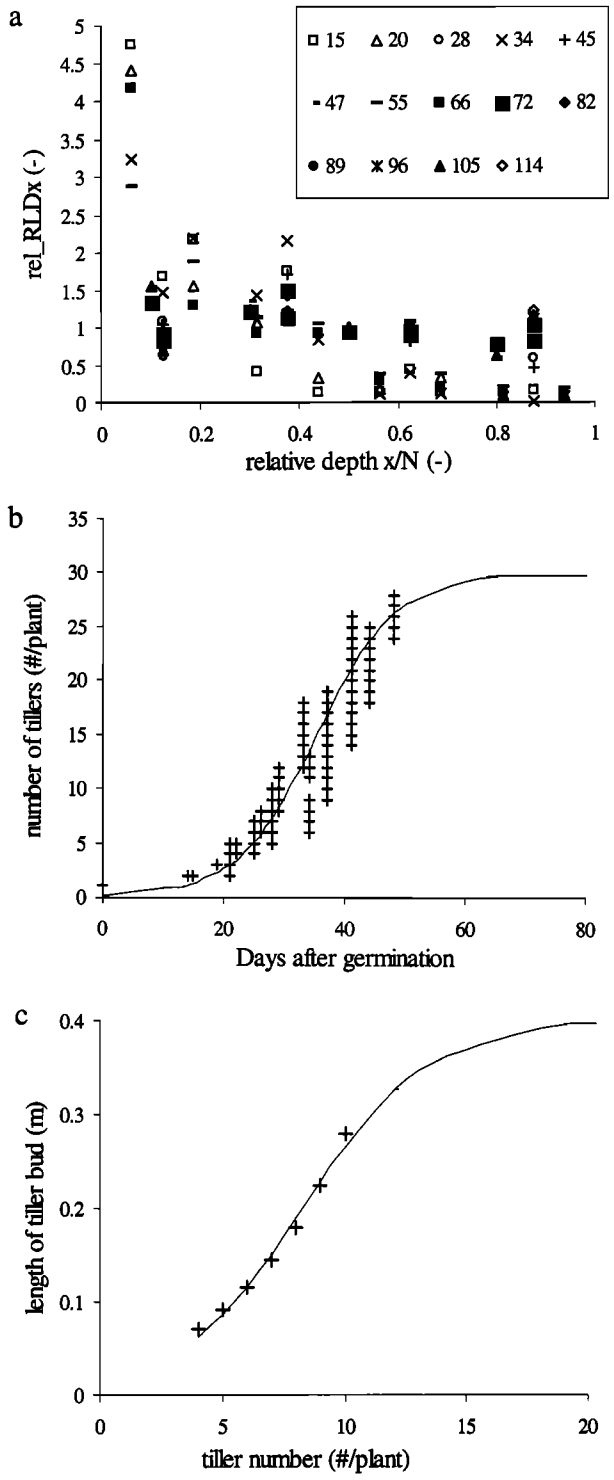

Figure 3. Plant parameters for (a) depth distribution of root length density from a data compilation from *Teo et al.* [1995], *Kang et al.* [1994], *Slaton et al.* [1990] and *Beyrouty et al.* [1988] using data from various days after transplanting (indicated in the legend), (b) fit (line) and measurement (pluses) of the number of tillers in time, and (c) fit (line) and measurement (pluses) of the tiller bud length as a function of tiller number.

Tanaka et al. [1995] found that on average 83-90% of the total root length constituted of lateral roots, and *Yamauchi et al.* [1987] found a contribution of 96%. It is estimated that the root tip forms 5.4% of the primary root, based on the

Table 2. Measured and Modeled Root Length Density Distribution with Soil Depth[a]

Soil Depth, cm	Measured RLD_x	Measured $rel(RLD_x)$	Modeled $rel(RLD_x)$
0-4	1.72×10^5	1.45	1.54
4-8	1.45×10^5	1.23	1.19
8-12	9.7×10^4	0.820	0.922
12-16	5.9×10^4	0.499	0.713

[a]The total root length density (RLD_x in m m^{-3}) in a soil layer and the relative root length density in a soil layer ($rel(RLD_x)$, dimensionless) are shown.

observation that 94.6% of an individual primary root is aerenchymous and the fact that root tips are not aerenchymous [*Beyrouty et al.*, 1988]. Based on these observations F_{exch} will vary between 0.84 and 0.96. For the model, 0.90 is chosen as a default value.

The *root length* is the average individual root length in a layer (in meters) and is estimated, assuming that roots are small chimneys that cross a soil layer with a certain tortuosity, as

$$root\,length = \frac{soil\,layer\,thickness}{\tau_r}. \quad (9)$$

Root tortuosity, τ_r, is estimated at 0.56 m soil m^{-1} root using data of *Denier van der Gon and Neue* [1996]. From the *root length*, one can calculate z_r as

$$z_r = \frac{root\,length}{2}. \quad (10)$$

The root cross section area over which diffusion takes place, $A_{r(x)}$, is given by

$$A_{r(x)} = number\,of\,roots \cdot \pi \cdot (R_r)^2. \quad (11)$$

R_r is calculated to be on average 0.28 10^{-3} m, based on a root radius for primary roots of 0.9-1.5 mm [*Yu et al.*, 1995] and a lateral root radius of 0.1 mm, calculated from *Drenth et al.* [1991]. The *number of roots* in a layer x is a function of RLD_x and is thus a dynamic parameter:

$$number\,of\,roots_x = \frac{RLD_x \cdot soil\,layer\,thickness \cdot A_s}{root\,length}. \quad (12)$$

3.1.3.3. Tiller characteristics, A_t and z_t. The shoot-cross section area over which diffusion takes place, A_t, is given, analogous to the root cross section area, by:

$$A_t = number\,of\,tillers \cdot \pi \cdot (R_t)^2. \quad (13)$$

R_t was measured for rice plants of the same rice variety by Groot et al. (2001) and the average value of 3.2 10^{-3} m is used as default in the model. The *number of tillers* is a function of time and was monitored while growing rice plants in the growing chamber. The growth curve of the number of tillers was fitted using a universal logistic growth curve:

$$number\,of\,tillers = \frac{maximum\,number}{1 + K_{til(no)} \cdot e^{-rgr_{til(no)} \cdot t}}; \quad (14)$$

maximum number is the maximum possible number of tillers and is estimated at 31 (number per plant), similar to data of *Watanabe and Kimura* [1995]. $K_{til(no)}$ and $rgr_{til(no)}$ were fitted to our tiller number observations (Figure 3b) at 31 and 1.5×10^{-6} s^{-1}, respectively.

The diffusion length through the tiller, z_t, is half the distance from the root-shoot interface to the micropores. The micropores are located around the top gap between the epidermis of the culm and leaf sheath [*Nouchi and Mariko*, 1993]; z_t can thus be assumed to be half the length of a tiller bud. This length depends on the time of tiller emergence. The later the emergence, the longer the tiller. The time it takes for a tiller to become fully developed is equal to the time needed to form two new tillers [*Hanada*, 1995]. Neglecting this growing period, the average tiller bud length only depends on the number of tillers. The average tiller bud length was fit by a universal logistic growth curve:

$$tiller\,bud\,length = \frac{maximum length}{1 + K_{til(length)} \cdot e^{-rgr_{til(length)} \cdot tiller\,number}} \quad (15)$$

maximum length is the maximum possible length of a tiller bud, estimated at 0.40 m (personal observation). $K_{til(length)}$ and $rgr_{til(length)}$ were fit at 26.1 and 0.394 tiller number^{-1}, respectively. A comparison with observed data is given in Figure 3c.

A mass balance for SF_6 is included in the computer model and never showed relative deviations >10^{-6}. Time steps in the model are determined by the characteristic time of the fastest flow, which is the flow in root and shoot (see section 4.1). The calculation of the amount of gas released in time is used for model validation. Statistical differences between model outcomes, for both validation and sensitivity analysis, and experimental observations were tested using a paired Student's t test.

3.2. Estimation of SF_6 Diffusion Coefficients

The prediction of SF_6 gas transport was limited by two unknown parameters, τ_f and the D_w for SF_6. Both parameters were estimated simultaneously by a measurement setup without a plant, described in section 2. For both experiments an effective diffusion coefficient (D_{eff}) can be related to the transport characteristics according to

$$\frac{total\,thickness}{D_{eff}} = \frac{filter\,thickness}{D_w \cdot \theta_f \cdot \tau_f} + \frac{soil\,thickness}{\frac{\varepsilon_S D_a \cdot \tau_a}{\alpha} + \theta_s \cdot D_w \cdot \tau_w} + \frac{water\,thickness}{D_w}. \quad (16)$$

All thicknesses were measured (in meters); θ_s was measured (0.57 m^3 water m^{-3} soil) and τ_a, τ_w, θ_f, and α were known. D_{eff} was estimated numerically with equations (1), (2a), (3), and (4), applying a constant D_{eff} throughout the system. Only simulations in which the differences between model and experiment were not significant according to a paired Student's t test (P > 0.05) were considered. The range of D_{eff} values was different in the two experimental replicates, because of the different soil and water thicknesses. The two unknown parameters, τ_f and D_w, could then be solved analytically by substitution in combination with equation (16), using the two ranges of D_{eff}. This yielded as significant combinations a SF_6 diffusion coefficient in water of 1.31 ± 0.04 10^{-9} m^2 s^{-1} (at T = 303 K) and a τ_f of 2.78 ± 0.62 m filter m^{-1} water. The results of the two experiments and (not significantly different (P > 0.05)) modeled SF_6 release using the average calculated τ_f and D_w are shown in Figure 4.

Temperature dependence of D_w is calculated with a Q_{10} value. The Q_{10} value is given the value of 1.31, analogous to *Segers and Leffelaar* [2001], after comparison with the temperature dependence of common atmospheric gases. The

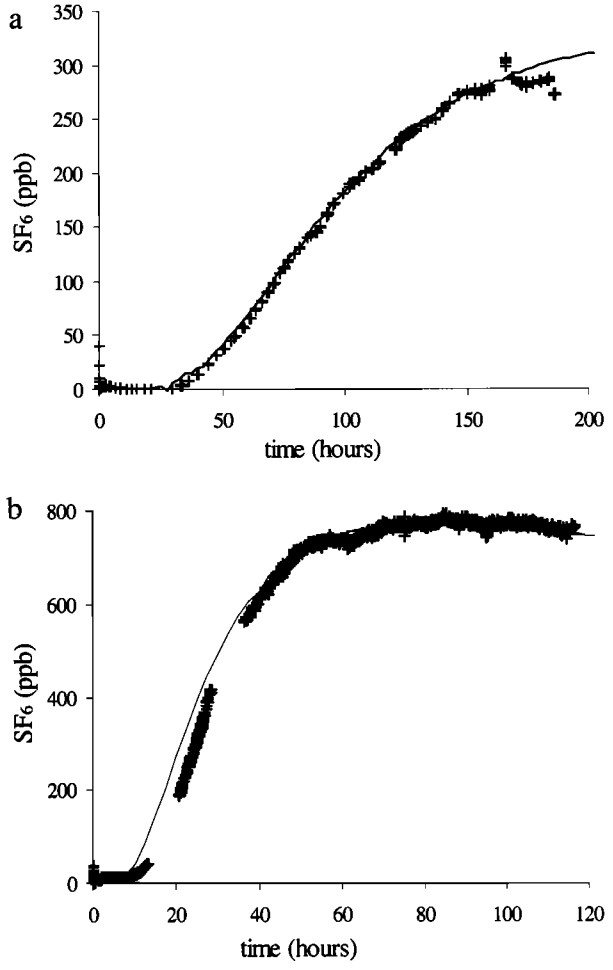

Figure 4. Fit (lines) of diffusion coefficient to measured concentrations of SF_6 (pluses) for (a) the first experiment, and (b) the second experiment.

diffusion coefficient of SF_6 in air at any temperature is calculated from the binary diffusion coefficients using the formulations and parameter values given by *Hirschfelder et al.* [1964].

4. Results

4.1. Model Validation

With the determination of the diffusion coefficients, all parameters to describe the soil-plant system are known. The average transmissivities for the different compartments for the first model validation experiment are presented in Figure 5. The transmissivities for the root compartment (except for the upper root layer that includes the root-shoot interface) and the shoot compartment are much higher than transmissivities of other compartments. The transmissivities show that diffusion through the rice plant is not the rate-limiting step, as was suggested already by *Lee et al.* [1981] and *Armstrong and Gaynard* [1976]. The transmissivity for the soil compartment itself is much lower than the combined transmissivities for the soil-root interface, root and shoot compartments, even though the soil transmissivity was weighed with the contribution of each soil layer to gas transport. At default conditions, most gas enters the root in the lower 2-3 cm and therefore they contribute most to the total transmissivity (thus decreasing the total diffusion distance). In addition, concentration gradients are much smaller within the soil than between soil and root (results not shown). This explains why most of the gas produced in the soil (e.g., methane) is emitted via plant-mediated transport, given that the root system is well developed [e.g., *Schütz et al.*, 1989]. The transmissivity and the concentration gradients for the soil compartment are by far the smallest and thus the rate-limiting step in gas transport through the soil-plant system. The transmissivity for the soil-root transport is the second rate-limiting step. This shows, in accordance with the suggestion of *Jackson and Armstrong* [1999], that the root surface represents a major gas transport resistance.

Transport limitations due to diffusion in soil and water are more severe than those at the water-air interface or at the tiller-air interface. It thus seems improbable that the use of closed chamber techniques for gas emission measurements will lead to major artifacts in measured gas release rates.

The results of the two validation experiments are shown in Figure 6. The SF_6 concentration follows a pattern similar to the diffusion experiments without a rice plant. The model predicts the gas transport through the soil-plant system with reasonable accuracy without fitting any parameter and using only default settings. Differences between model and experiment were not significant ($P > 0.05$) for either of the two validation experiments. If the plant presence is neglected, diffusion rates are severely underestimated, because the plant-mediated transport pathway is blocked (results not shown). Inclusion of the characteristics of the plant system is thus necessary for the prediction of gas flows. On the other hand, gas transport rates are only slightly increased (data not shown) if it is assumed that conductivity through the plant is infinite and thus the gas is released into the atmosphere as soon as it enters the plant. These results can be understood from the transmissivities shown in Figure 5.

Measured gas concentrations in Figure 6a show distinct spikes. An increase in SF_6 concentrations occurred within 2 hours after the light was turned on, and a downward spike was found after the light was turned off. Equilibrium was obtained within a few hours, and the SF_6 signal represents

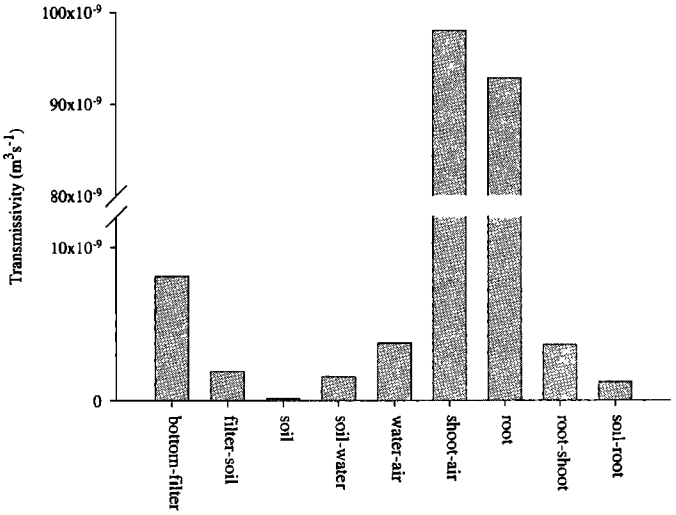

Figure 5. Overview of all transmissivities, κ (m^3 s^{-1}), calculated by the model (equations 2) at default parameter values.

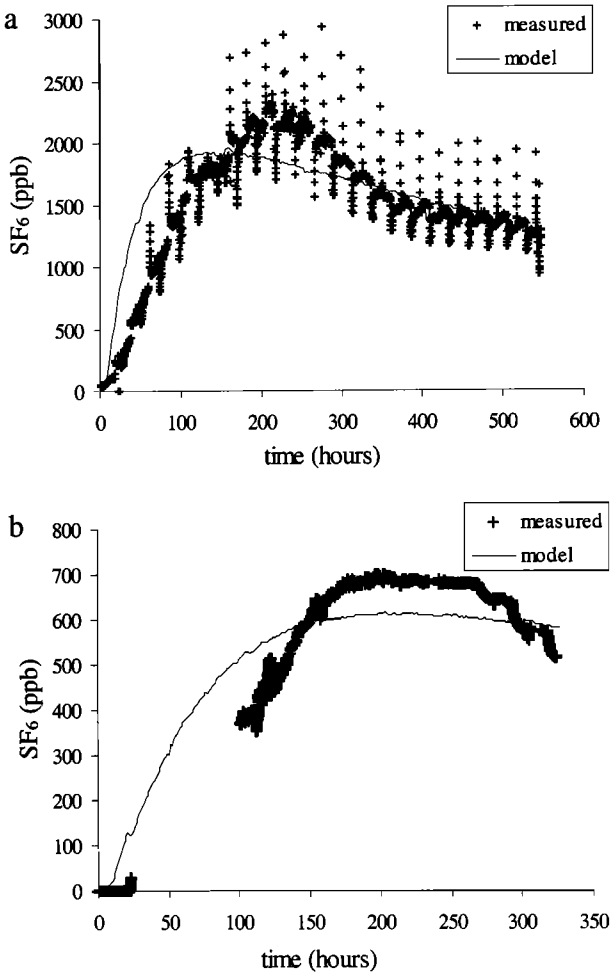

Figure 6. Measured (pluses) and modeled (line) changes in SF_6 concentrations in time in (a) the first validation experiment, and (b) the second validation experiment. Modeled concentrations were calculated with the default settings of the model.

real emission values while an equilibrium was present. Similar spikes occurred when the temperature was increased artificially by 5°C, excluding direct effects of light radiation (data not shown).

In the second validation experiment the flow inlet had been moved to the bottom of the headspace. This resulted in an immediate mixing of the air within the headspace and avoided spike formation (Figure 6b). This indicates that the spikes were not caused by changes in the diffusion coefficient or solubility with temperature, but probably because the headspace compartment had not been mixed properly in the first validation experiment, even though there had been a continuous flow. It seems that at a temperature increase, mixing with the lower part of the compartment increased, leading to a release of accumulated SF_6. At the moment the light was turned off and temperature decreased, mixing decreased as well and a new equilibrium was formed after some time.

In both validation experiments, the measured SF_6 signal started to increase later than the modeled SF_6 release. This could have been caused by the method of injecting SF_6. Gaseous SF_6 had been added to the bottom space and the gas dissolved by stirring. The temporary presence of small gas bubbles underneath the filter may have retarded gas diffusion.

4.2. Model Sensitivity Analysis

The model presented in this paper describes gas transport in a soil-plant system as mechanistically as possible. It can predict SF_6 release reasonably well without fitting any experiment specific parameter. Some plant parameters were estimated from a general expression including the time after germinating in combination with the total aboveground biomass. Other plant parameters were derived from published data. Soil transport characteristics were estimated either from published data or from experiments independent of the validation experiments. Even though no parameter fitting was performed, it is important to understand the sensitivity of gas transport to the various parameters, because many parameter values are variable or uncertain. Only parameters influencing transport processes with low conductances will affect SF_6 release. From Figure 5 it follows that SF_6 release is relatively insensitive to processes within tillers and roots. These processes were therefore not studied in our sensitivity analysis. We focused on effects of the exchange surface of the roots, the diffusion coefficient of SF_6 in water, the conductance at the root-shoot interface, and the effects of different distributions of RLD_x. The latter is of importance for the determination of $\kappa_{s,r(x)}$. All variables were varied one at a time within the range estimated from experiments and published data. For comparison, we used data from the first validation experiment, because this experiment had an uninterrupted measurement series.

4.2.1. Effects of root fraction permeable to gas, F_{exch}. Only lateral roots and root tips contribute to gas exchange at the root surface. The influence of increasing F_{exch}, which is almost equivalent to the sensitivity for a variation in root radius, is small (Figure 7a), and one might as well assume that the complete root surface is active in gas exchange. The total root surface is largely determined by the lateral roots (leading to a default setting for F_{exch} of 0.90). Only if F_{exch} is decreased below 0.8, thus assuming that there are only primary roots in the system, then the system's response is modified without improving the transport description and differences between model and experiment become significant ($P < 0.001$). Such low F_{exch} values are, however, not likely to be encountered in nature. The system is not sensitive to F_{exch} if F_{exch} is kept in a reasonable range.

4.2.2. Effects of diffusion coefficient of SF_6 in water, $D_{w,SF6}$. An error of 3% in $D_{w,SF6}$ was found in the experiments without plants, based on our error analysis. With the sensitivity analysis, the effects of a change of ±5 and 10% in the default estimate of 1.31×10^{-9} m^2 s^{-1} were tested. These changes resulted in major differences in the systems response (Figure 7b). Only for the default $D_{w,SF6}$ and for a 5% smaller $D_{w,SF6}$, the differences between model and experiment were not significantly different ($P > 0.05$). The large influence can be understood from Figure 5, which shows that the transport through the soil is the rate-limiting step. An increase in $D_{w,SF6}$ overestimates transport during large periods of the incubation. A decrease in $D_{w,SF6}$ describes the response slightly better at the start but poorer than the default settings in the central period of the incubation. Given the error in the estimation of $D_{w,SF6}$ and the large response of gas transport to changes in $D_{w,SF6}$, there is a need for better experiments to determine $D_{w,SF6}$.

A small change in temperature can easily alter D_w by 5 or 15%. Such alterations in D_w modify gas emission patterns more than proportionally (Figure 7b), although less than estimated by the conductance predictions of *Hosono and*

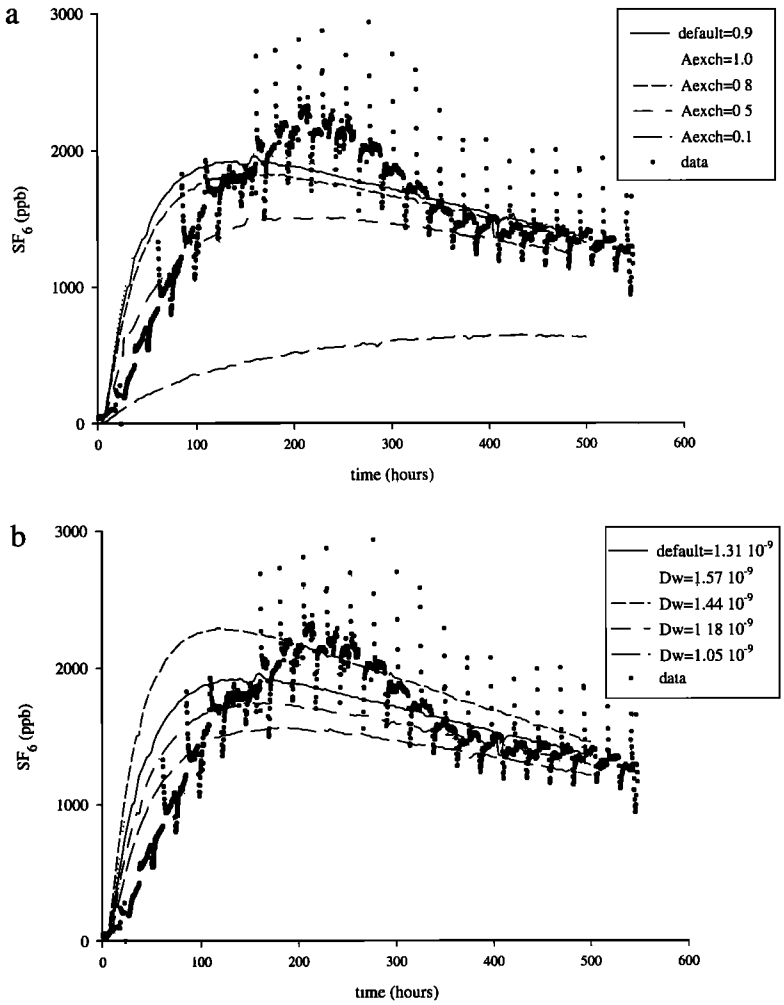

Figure 7. Sensitivity analysis of the model. The sensitivities were tested against measured values for (a) the fraction of the root surface active in gas exchange (F_{exch}), (b) estimation of the diffusion coefficient of SF_6 in water at T = 303 K (D_w), (c) different estimates for the conductivity at the root-shoot interface of the rice plant ($\omega_{r,t}$), and (d) different root distributions. Two extremes, a uniform distribution with depth and a root distribution with depth as it is at the start of the season, and their intermediates were tested.

Nouchi [1997]. These alterations in D_w may, due to its sensitivity, contribute considerably to the diel emissions patterns found for methane emissions [e.g., *Nouchi et al.*, 1994].

4.2.3. Effects of root-shoot conductance, $\omega_{r,t}$. Although the low conductance at the root-shoot interface is by far the most important resistance for plant transport within the plant and one of the lower transmissivities in the complete soil-plant system, the effects of a change in $\omega_{r,t}$ are small (Figure 7c) and insignificant ($P > 0.05$). The values for $\omega_{r,t}$ were varied within the range encountered in experiments (Groot et al., 2001), but the system was almost insensitive to these changes. Probably the large transport resistances within the soil dominate gas transport rates.

Within the plant, however, the resistance introduced by $\omega_{r,t}$ is of importance. If there had been no transport limitation within the plant, then gas concentrations within the plant would have been similar to ambient concentrations. In reality, gas concentrations within the plant, e.g., for methane, are much higher than ambient concentrations [*Byrd et al.*, 2000].

4.2.4. Effects of root length distribution with depth, *rel(RLD$_x$)*. An average fitted *rel(RLD$_x$)* was used in the model. This distribution was estimated from published data and tested for our validation experiment (Table 2). The differences with measured distributions were small but largest for the bottom layers, while these bottom layers contributed most to the gas exchange with the roots (and thus with the atmosphere). Given this difference and the plasticity of root distributions and the transport limitation induced by the transport between soil and root, the sensitivity for *rel(RLD$_x$)* was tested. The influence of different assumptions for *rel(RLD$_x$)* on measured gas release rates was very large (Figure 7d). All tested root distributions other than the default distribution yield significant differences between model and experiment ($P < 0.01$). Hardly any SF_6 is released at a root distribution that occurs at the start of the season with very few roots in the bottom layers (keeping the same total average RLD over the profile). With a uniform *rel(RLD$_x$)*, SF_6 release is increased, especially at the start of the incubation. This illustrates again, as would be expected on the basis of the transmissivities in Figure 5, the importance of the bottom layers for gas transport by providing a fast shortcut to plant-mediated transport. The differences in measured and predicted *rel(RLD$_x$)* for the bottom layers (Table 2) may thus

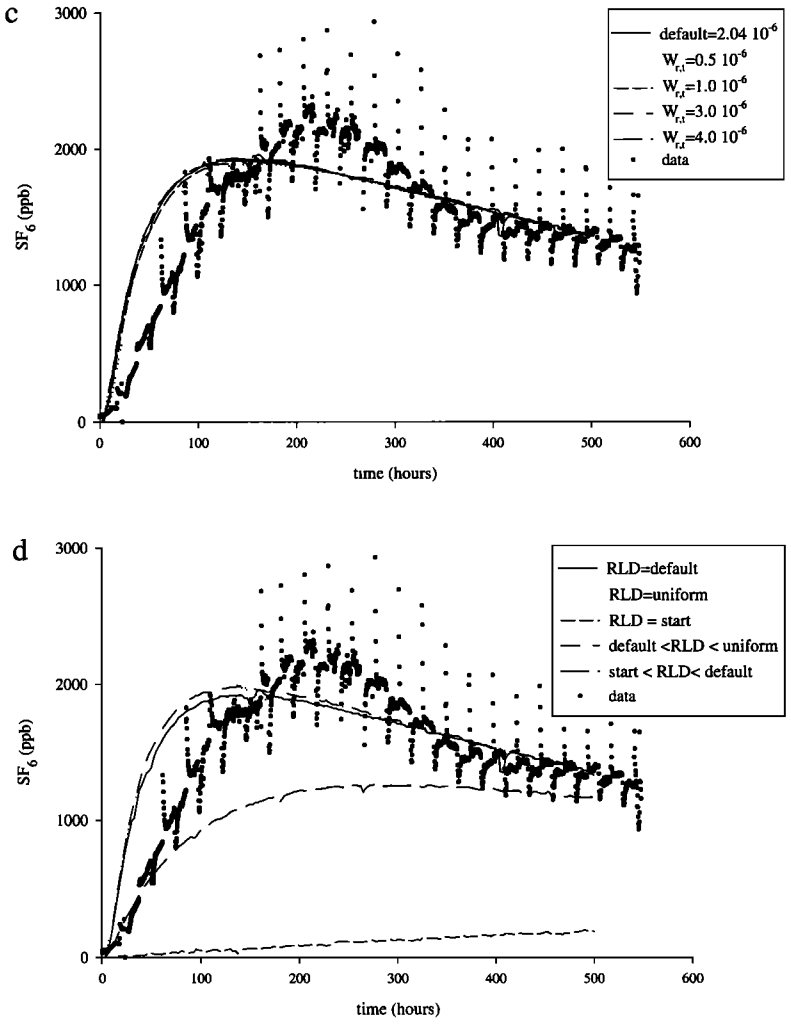

Figure 7. (continued)

have led to the differences in measured and predicted SF_6 release. Owing to the plasticity of *rel(RLD$_x$)*, it will be very hard to make a fully accurate prediction of the dynamics in gas release rates from soil-plant systems.

5. Conclusions

A fully mechanistic model based on diffusion equations for the gas transport in a soil-plant system of flooded rice is presented in this paper. The model combines transport descriptions within the soil with those within the plant and is more comprehensive than other published transport models. Model parameters were estimated from published data and experiments on the diffusion coefficient of SF_6. These default settings could reasonably predict gas release dynamics in a soil-plant system, in which gas was released at 17-cm depth. Such a depth of maximum gas production [*Frenzel et al.*, 1992; *Rothfuss and Conrad*, 1998; *Schütz et al.*, 1989] which is below the depth of maximum root density [*Frenzel et al.*, 1992] is common for CH_4 and to a lesser extent for H_2S. For these compounds, the model transmissivities explain why most gases are released via plant-mediated transport. The model shows the sensitivity of gas transport for $D_{w,SF6}$, while this parameter is sensitive to temperature changes. This might provide a (partial) explanation for diel patterns found for greenhouse gas emissions. The model also shows that the root-shoot interface represents the major resistance for gas transport within the plant.

However, also for gas compounds that are mostly produced in the upper few centimeters, like N_2O and CO_2, the model helps to understand and quantify rate-limiting steps in gas transport. The calculated transmissivities and concentration gradients at the default settings and the sensitivity analysis clearly show that the diffusion coefficient in soil, which was unfortunately not well constrained, and the root length density distribution are the limiting factors for gas transport. For compounds like N_2O and CO_2 this still applies, although in these cases the horizontal, instead of vertical, diffusion to the nearest root will be important. This implies that for these compounds the root length density distribution becomes even more important. Unfortunately, these root distributions are mostly not known, while even a small deviation in distribution can cause deviations between modeled and measured gas transport, as was shown by the validation experiments and the sensitivity analysis. Given the uncertainty and the plasticity of *rel(RLD$_x$)*, it will be difficult to predict quantitatively the in situ rates of gas transport, but the model and the transmissivities provide a tool for understanding gas transport patterns.

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